

Social learning is central to innovation, in primates and beyond

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Abstract: Much of the importance of innovation stems from its capacity to spread via social learning, affecting multiple individuals, thus generating evolutionary and ecological consequences. We advocate a broader taxonomic focus in the field of behavioral innovation, as well as the use of comparative field research, and discuss the unique conservation implications of animal innovations and traditions.

We agree with Ramsey et al. on the importance of an operational definition of innovation. This will clarify communication and direct our focus to significant examples of innovation for closer analysis. However, we suggest a shift in the emphasis. It is useful, as Ramsey et al. do, to discriminate between novel individual innovation versus socially learned behavior. However, they focus on the former to the extent that social learning is

primarily considered something to discard in the search for examples of “true” (purely individual) innovation. Ramsey et al. define innovation as a process and product attributable to a single individual. To this end, they exclude social learning from the phenomenon they define and discuss. Individual innovations are certainly interesting and worthy of study. However, the importance of innovation stems mostly from its capacity to spread via social learning.

Although ultimately originating from single individuals, innovations become most important when they transcend their solitary origins and become more prevalent. As the authors point out, innovation is a key component of most definitions of culture, and is important because it can affect a species’ ecology and evolution. In both respects, innovations are relatively insignificant when restricted to a single individual. An innovation can become part of a culture only through social learning. Likewise, innovations are important factors in the ecology and evolution of a species only when shared by many individuals. Although it may be possible for multiple individuals to independently produce similar innovations, this is not what we typically see in nature. Instead, when innovations become sufficiently widespread to play an essential role in a species’ ecology and evolution, they usually have done so through social learning (Laland & Hoppitt 2003; Laland & Janik 2006; Mann & Sargeant 2003; Yurk et al. 2002).

There are important benefits to a broad taxonomic scope in the study of animal innovation. Primates are of special interest to anthropologists because of their relatedness to humans. However, some of the most important questions surrounding the capacity for innovation concern its evolutionary origins and consequences and its ecological effects. The most powerful tool in biology for addressing such questions is the comparative

method (Freeman & Herron 2004; Harvey & Purvis 1991; Perry 2003). The strength of comparative analysis depends on how many taxa and independent origins are considered for the phenomenon of interest. Primates present many of the best-known examples. However, animal innovation is taxonomically widespread, and other groups are also noteworthy for the frequency and importance of behavioral innovation. We discuss two examples next. Incorporating as many taxonomic groups as possible in our consideration of innovation can greatly increase the strength and generality of our inferences.

Cetaceans (toothed whales and dolphins) have exceptionally large brains, high levels of intelligence, mental flexibility, and a capacity for behavioral innovation (Marino et al. 2007). Field studies on wild cetaceans have revealed a diversity of behavioral traditions apparently derived from individual innovations (Rendell & Whitehead 2001). As is true of primates, many behavioral traditions in bottlenose dolphins (*Tursiops truncatus*) involve specialized foraging techniques (Chilvers & Corkeron 2001), and some also involve tool use (Mann & Sargeant 2003). To date, the best information comes from one long-term field study (Mann & Sargeant 2003). Through comparison across multiple populations, we could better understand which behaviors are instinctive or environmentally induced, and which are valid examples of innovations that have become distinct local traditions. Clearly, there is opportunity for such comparative field study in this species, as several potential examples of behavioral traditions and innovation have not yet been investigated. For example, many unusual foraging specializations have been identified in various populations of bottlenose dolphins in and around the Gulf of California (Leatherwood 1975).

Behavioral innovations are well documented in crows (*Corvus* spp.) and other

corvids (Emery & Clayton 2004). Examples include tool use in wild populations, with evidence for social transmission and cumulative social evolution (Hunt & Gray 2003). It has been proposed that corvids and apes share the same “cognitive toolkit,” including abilities for causal reasoning, prospection, imagination, and flexibility (Emery & Clayton 2004). The reason that similar cognitive traits have evolved in both groups may be that both needed to solve similar socioecological problems, including locating and exploiting unpredictable food resources, and understanding relationships among individuals in large social groups (Emery & Clayton 2004). Similar selective pressures have also been implicated in the evolution of the cognitive abilities of cetaceans (Marino et al. 2007).

Although both have their strengths, comparative field research offers several advantages over captive studies for investigating innovations. Ramsey et al. stressed field studies at the beginning of their article, yet promoted captive studies for confirming innovations. Captive studies can only determine the degree to which a behavior is instinctive, but cannot usually confirm that a particular behavior is an innovation in wild populations. Moreover, the ecological and evolutionary implications of captive studies can be difficult to interpret because of the altered and restricted physical and social environment, especially considering the fact that behavior in large-brained social animals is very sensitive to context (Rendell & Whitehead 2001). Such species are precisely where Ramsey et al. predict finding more innovation. Laboratory experimentation facilitates isolating behavioral variables, whereas field studies examine these variables in their evolutionary context (Bateson 2003; Perry 2003; Smith et al. 2002; Whiten et al. 2005).

The existence of behavioral innovations maintained through social learning, could

have a large impact on conservation efforts by giving distinct conservation significance to each unique population. Complementary to the importance of protecting genetic pools, the preservation of behavioral traditions could add a new dimension to conservation priorities and strategies (Whitehead et al. 2004).

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